'Chloride cells' in the gills of fresh-water teleosts

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With 2 plates (figs. 1 and 2)

Summary

Specialized cells of several kinds, namely, (a) mucous-gland cells, (b) large bi- or trinucleate glandular cells, and (c) mast cells occur in the gills of some species of fresh-water teleosts.

The typical 'goblet' type of mucous glands are present in large number in fresh-water species, such as *Catla catla*, *Labeo rohita*, *Ophiocephalus punctatus*, and *Mastacembalus armatus*. In *Catla catla*, these glands respond to the 'chloride test'. This indicates that, besides discharging mucus, they also play some part in the elimination of chloride. In *Ophiocephalus punctatus*, *Clarias batrachus*, and *Heteropneustes fossilis* only some of the mucous cells give a positive reaction with the AgNO₃/HNO₃ test for chloride. This may mean that a few of them are in a state of active secretion of chlorides, while others are in a non-secretory phase.

Large eosinophil glands with 2 or 3 nuclei also occur, chiefly in the siluroids. The function of these hypertrophied multicellular glands is not clear.

Judged by the AgNO₃/HNO₃ test, *Catla catla* possesses the highest number of chloride cells. In *Hilsa ilisha*, *Rita rita*, *Ophiocephalus striatus* and *Mastacembalus armatus*, only a 'network of silver' exists on the surface of the primary and secondary lamellae.

The 'chloride cells' are said to be a characteristic of marine fishes in which an extrarenal mechanism for the elimination of excess of salts from the body fluid is necessary for correct osmo-regulation. These cells are also said to make their appearance in fresh-water fishes that have been experimentally subjected to a saline medium. The presence and occurrence of 'chloride cells' in fresh-water fishes living in their natural habitat is, therefore, interesting. The discovery of the presence of actively secreting chloride cells in certain species of fresh-water teleosts and their mucoid nature are new results reported here.

Introduction

It has been claimed that the bulk of the sodium, potassium, and chloride absorbed in the gastro-intestinal tract of marine teleosts is excreted by the 'chloride-secreting' cells in the gills (Smith, 1930; Keys, 1931, 1933; Keys and Willmer, 1932); but Bevelander (1935, 1946) believed that the supposed excretory cells are nothing but intra-epithelial mucous glands and that the general respiratory epithelium might be a site of chloride excretion.

Liu (1942) attempted to acclimatize the fresh-water air-breathing fish, *Macropodus opercularis*, to different concentrations of salt solution. He stated that even an exclusively fresh-water fish can tolerate a salt solution nearly as saline as sea-water by virtue of the enormous development of latent 'chloride-secreting cells'. From this experiment he concluded that fresh-water teleosts possess 'chloride-secreting cells' in the gills in a dormant condition.

Copeland (1948a, b) noted cytological changes in the chloride cells of *Fundulus heteroclitus* during adaptation to varying degrees of salinity, and by using

the Leschke test demonstrated the presence of a copious amount of chloride
in the secretory cells of fishes adapted to the salt-water condition, but only
a limited amount of it at the free ends of the cells in fishes adapted to fresh-
water life. Getman (1950) working on Anguilla rostrata came to a similar
conclusion.

More recently Vickers (1961) has said, with reference to the gills of Lebistes
reticulatus (a fresh-water teleost), that after subjection to hypertonic-salt
solutions of varying concentrations, its mucous cells become functionally
transformed into chloride cells.

The present studies on gill epithelia of fresh-water teleosts were undertaken
in order to remove some of the ambiguities and deficiencies in our knowledge.

Materials and methods

Fishes were collected from the river Ganges and the local ponds. Pieces of
their gills were immediately fixed in Zenker, Helly, chrome-Bouin, alcoholic
Bouin, Gilson’s mercuro-nitric, or Carnoy’s fluid after gently removing the
adhering mucus with a cotton swab and rinsing them in river water. Sections
of the gills were stained with Heidenhain’s or Delafield’s haematoxylin or
Mayer’s haemalum, and counterstained with eosin. Mallory’s triple stain,
borax-carmine followed by picro-indigo-carmine, and other stains were also
employed.

Parts of the gill lamellae were dissociated in several different fluids such as
sodium-chloride solution, Ranvier’s alcohol, and borax solution. The disso-
ciated cells were stained with methylene-blue and examined with the
microscope.

Thionin was used to demonstrate the presence of mucus and mucus-
producing cells and mast cells (the latter by their chromotropic reaction).
Sections were stained in a 0.2% aqueous solution of thionin, quickly passed
through acetone to xylene, and mounted in balsam. The PAS technique was
used to demonstrate the mucus-producing cells. Fresh tissues of the gill
lamellae were also studied supravitally with neutral red.

The Leschke silver technique, as modified by Copeland (1948a, b), was also
used to detect the presence of the chloride in the so-called branchial glands.

Histological studies were made on the following species of fishes:

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Result of chloride test</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Group A</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Hilsa ilisha (Ham.)</td>
<td>Clupeidae</td>
<td>Done</td>
</tr>
<tr>
<td>2. Gadusia chapra (Ham.)</td>
<td>„</td>
<td>Not done</td>
</tr>
<tr>
<td><strong>Group B</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. Catla catla (Ham.)</td>
<td>Cyprinidae</td>
<td>Done</td>
</tr>
<tr>
<td>4. Labeo rohita (Ham.)</td>
<td>„</td>
<td>Not done</td>
</tr>
<tr>
<td>5. Rohtee cotto (Ham.)</td>
<td>„</td>
<td>Not done</td>
</tr>
</tbody>
</table>
**Species**  | **Family**  | **Result of chloride test**
--- | --- | ---
6. *Clarias batrachus* (Linn.) | Clariidae | Done
7. *Heteropneustes fossilis* (Bloch) | Heteropneustidae | Done
8. *Wallago attu* (Bl. & Schn.) | Siluridae | Not done
9. *Rita rita* (Ham.) | Bagridae | Done
10. *Mystus aor* (Günther) | | Not done

**Group D**
11. *Ophiocephalus punctatus* (Bloch) | Ophiocephalidae | Done
12. *Ophiocephalus striatus* | | Done

**Group E**
13. *Anabas testudineus* (Bloch) | Anabantidae | Not done
14. *Trichogaster fasciatus* (Bl. & Schn.) | Osphronemidae | Not done

**Group F**
15. *Mastacembalus armatus* (Lacep.) | Mastacembelidae | Done

The chloride test was only applied to nos. 1, 3, 6, 7, 9, 11, 12, and 15 in the above list.

**Results**

The principal findings are summarized in tables 1 and 2 (see appendix, p. 88), and illustrated in figs. 1 and 2.

The structure of the gills of *Labeo rohita, Hilsa ilisha, Rita rita,* and *Ophiocephalus striatus* has been recently described in detail by myself (1960). In the following pages the branchial glands of *Catla catla, Heteropneustes fossilis, Ophiocephalus punctatus,* and *Mastacembalus armatus* are described in detail.

**Catla catla**

In this species only two kinds of specialized cells are present, the mucous glands and the acidophil mast cells.

Mucous glands are present in large numbers in the epithelium covering the gill arches and the primary and the secondary gill lamellae. In a horizontal section of the epithelium of the head of the gill arch, the mucous glands are found to be unicellular and rounded, and to possess flattened nuclei owing to the presence of the secretory substance. The glands are scattered on the general surface of the primary gill lamellae and in the interlamellar space close to the base of the secondary lamellae (fig. 1, $F$). A few of them may occur on the secondary lamellae as well.

A paper on the mast cells of this and other species was communicated by myself to the Second All-India Congress of Zoology held in Varanasi (Munshi, 1962).

In *Catla catla,* a number of epithelial cells of the primary lamellae react to the AgNO$_3$/HNO$_3$ test for chlorides. In fig. 2, a the black marks present in the inter-lamellar area, at the bases of the secondary lamellae, represent epithelial cells that have responded to this test. Under higher magnification, the outline and shape of these cells can be made out (fig. 1, $E$). Some of them
react strongly to this test, proving thereby the presence of chlorides in them. These darkened cells occupy the same position as that occupied by the mucous glands.

It seems that the mucous glands present on the primary-gill lamellae and those lying between the bases of the secondary lamellae are concerned with the excretion of chlorides also. The exact parallelism between the position of the mucous glands in fig. 1, F and the incidence of the chloride-secreting cells in fig. 1, E is a pointer in this direction. These cells react metachromatically with thionin and give a positive reaction with PAS.

**Heteropneustes fossilis**

In this species large acidophil-gland cells and mucous glands are present. The large acidophil-gland cells are present in the epithelium covering the surface of the gill-arches. They are larger than the other epithelial cells of the gill (fig. 1, A). Most of the cells show 2 zones, the central one clear and containing the nuclei and the outer one staining more darkly. Similar acidophil-gland cells also abound in the epidermis of the skin of *H. fossilis*.

The mucous glands are abundant in the epithelium covering the head of the gill arches and occur in smaller numbers on the primary gill lamellae. However, these glands are absent from the secondary lamellae.

**Result of chloride test**

A number of epithelial cells of the primary-gill lamellae respond to the chloride test. Fig. 2, B shows the general distribution of the responsive cells borne by the gill lamellae. But all the epithelial cells do not react to the chloride test, and this indicates that certain of the epithelial cells are specially concerned in eliminating chlorides.

**Ophiocephalus punctatus**

In this species only 2 kinds of specialized cells, namely mucous glands and acidophil mast cells are present in the gills.

Mucous glands are present in the epithelium covering the heads of the gill arches and the primary and the secondary gill lamellae (fig. 1, C). Each
FIG. 1

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FIG. 2
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mucous gland is a unicellular, flask-shaped structure, opening to the exterior through a small pore. These glands are also found on the primary lamellae at the bases of the secondary lamellae and may occur even in the secondary lamellae (fig. 1, c). They give a strong reaction with PAS, showing thereby that the secretory substance is a mucopolysaccharide (fig. 2, d, e).

Some of the epithelial cells of the primary and the secondary lamellae respond to the chloride test (fig. 1, d). Those occurring at or near the bases of the secondary lamellae are prominent in form and react sharply to the AgNO₃/HNO₃ test. Sometimes they appear to be vesicular, with a spout-like opening. It seems probable that some, if not all, of the mucous glands are capable of acting as chloride-excreting cells (compare fig. 1, c with fig. 1, d).

**Mastacembalus armatus**

In this species only the mucous type of cells are found. Mucous glands are present in the epithelium covering the heads of the gill-arches and the primary and the secondary gill lamellae (fig. 2, c). They are of the usual goblet type. They are abundant and lie close to one another, forming almost a continuous layer over the head of the gill-arch. In the primary, and more particularly in the secondary lamellae, they exist in a hypertrophied condition. Each is a unicellular gland containing finely granular cytoplasm and a nucleus displaced to one side. The cytoplasm of these glandular cells is eosinophobe.

Neither the epithelial cells nor the mucous glands respond to the AgNO₃/HNO₃ test for chlorides. This shows that the specialized mucous glands present in the gill region are not concerned in the work of chloride excretion. Occasionally, a 'silver network' is formed on the surface of the primary and the secondary gill lamellae. Obviously this is due to the presence of chloride in the inter-cellular matrix (fig. 2, f).

**Discussion**

It may be useful to list here the characters of the 'chloride cells', according to the descriptions of the authors already mentioned.

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FIG. 2 (plate). A, a horizontal longitudinal section of the primary gill lamellae of *Catla catla* passing through the secondary gill lamellae of both sides, showing the presence of the chloride cells after the application of the AgNO₃/HNO₃ test for chlorides.  
B, a longitudinal section passing through several primary gill lamellae of *Heteropneustes fossilis*, showing the distribution of the 'chloride-secreting cells'. The chlorides extruded by the secretory cells have reacted to the AgNO₃/HNO₃ test and are seen as black dots.  
C, a horizontal longitudinal section of a primary gill lamella of *Mastacembalus armatus*, showing the presence of hypertrophied mucous glands (muc) on the secondary lamellae.  
D, a longitudinal section of a primary gill lamella of *Ophiocephalus punctatus*, showing the distribution of PAS-positive cells on the secondary gill lamellae.  
E, a transverse section of a primary gill lamella of *Ophiocephalus punctatus*, showing the position of the PAS-positive cells (mucous glands) in the epidermis.  
F, a section passing superficially across the surface of a primary gill lamella of *Hilsa ilisha*, showing the silver network formed after treatment with AgNO₃/HNO₃ for testing chlorides. The pores (pr) of the mucous glands are also clearly seen.
1. The cells are ovoid, or sometimes columnar (Copeland, 1948 a, b).
2. They are large.
3. Their cytoplasm is finely granular.
4. There is a marked affinity for eosin.
5. The nucleus is nearly spherical, and frequently eccentric (Liu, 1942, 1944).
6. The cells are present in the epithelium of the secondary and the primary lamellae. They are closely packed together in the epithelium of the filament, between the bases of the respiratory platelets (Getman, 1950). They may reach the sub-epithelial connective tissue layer.
7. They are close to the vascular layer. ‘The correlation between the number of chloride cells and the degree of vascularity is very well marked’ (Burns and Copeland, 1950).
8. They respond to the chloride test.
9. They are secretory (Keys and Willmer, 1932; Liu, 1942, 1944).
10. They give a strong reaction to the PAS test (as is shown in the present paper).
11. They give a chromotropic reaction with metachromatic dyes (present paper).

In a comparative study of the branchial epithelium of fishes, Bevelander (1936) found several types of ‘intra-epithelial gland cells’ which, according to him, belong to unicellular, multicellular, and transitional types. In the present study of the branchial glands of the fresh-water teleosts only 3 types of specialized cells have been found in the gills: the mucous glands of goblet type, the mast cells, and the large eosinophil, multi-nucleate gland cells. The multicellular type of branchial glands were described by Bevelander either as crescentic patches of cells, definitely oriented, with well differentiated tall columnar cells, or as typically pear-shaped or flask-shaped glands composed of closely-packed, tall columnar cells. These (multicellular) branchial glands of Bevelander closely resemble the ‘taste buds’ found invariably on the surface of the heads of the gill-arches (fig. 1, b) and in the branchial regions of the pharynx in fishes. As these organs are definitely sense organs, they have been omitted from consideration here. Branchial glands, possibly multicellular in composition, are represented by the large eosinophil glands that are bi- or tri-nucleate and are found chiefly in the siluroids (fig. 1, A). Such glands also abound in the integument of the siluroid fishes. The function of these hypertrophied-multicellular glands is not clear.

Mucous glands of the ordinary goblet type are present in large numbers in the gill epithelium of the fresh-water fishes examined, except in Trichogaster fasciatus. They generally occur on the head of the gill-arches and may even extend on to the surface of the primary gill lamellae. In certain cases, such as Catla catla, Labeo rohita, Ophiocephalus punctatus, O. striatus, and Mastacembalus armatus, they extend into the epithelial covering of the secondary gill lamellae. In the gill rakers of Labeo rohita a modified type of these glands
occurs, which may be looked upon as having been derived from the usual kind of mucous glands. The mucous glands of the primary lamellae of *Catla catla* respond to the 'chloride test', and this indicates that these glands, besides discharging mucus, also play a part in the process of elimination of the chlorides. In *Ophiocephalus punctatus*, *Clarias batrachus*, and *Heteropneustes fossilis* only a few of the mucous glands react positively to the AgNO₃/HNO₃ test.

The AgNO₃/HNO₃ test for chlorides was applied to several species of fishes. *Catla catla* showed the greatest number of chloride cells; the other species examined, in which the mucous gland cells reacted positively to a limited extent, were *Ophiocephalus punctatus*, *Clarias batrachus*, and *Heteropneustes fossilis*. In *Hilsa ilisha*, *Rita rita*, *Ophiocephalus striatus*, and *Mastacembalus armatus* only a network of silver is formed on the surface of the primary and the secondary lamellae. Recently Shelbourne (1957a, b) also obtained a similar kind of silver network in the integument of the marine plaice larva, which he took to mean that the excretion of chlorides also takes place through the general integumental surface. In the fishes reported here, the silver network is evidently caused by the presence of chlorides in the intercellular-cementing substance. The 'openings' of the mucous glands can be seen distinctly in the interstices of the network. Occasionally a little of the secretory matter containing chlorides is detectable in the small pores in the silver network. In *Catla catla* it is seen beyond doubt that ordinary mucous glands are capable of copiously excreting the chlorides in addition to mucus. *Ophiocephalus punctatus*, *Heteropneustes fossilis*, and *Clarias batrachus* also react like *Catla catla* to the AgNO₃/HNO₃ test, but to a lesser degree.

The specificity of the AgNO₃/HNO₃ test as a histochemical index of the presence of chlorides has been doubted by Lison (1936) and others. Copeland (1948a, b), however, believes the AgNO₃/HNO₃ test for chlorides to be dependable. Shelbourne (1957) has attempted to confirm the presence of silver chloride by using solvents of silver chloride.

According to the theory of osmo-regulation, extra-renal excretion of chloride is not to be expected in purely fresh-water teleosts like *Catla catla*, *Ophiocephalus punctatus*, *O. striatus*, *Clarias batrachus*, and *Heteropneustes fossilis*. The occurrence of 'chloride cells' in the gills of the fresh-water fishes is therefore paradoxical. Copeland (1948a, b) explains this away by saying that the cell reverses its polarity and serves as a physiological mechanism to absorb chloride ions from fresh water, and Krogh (1937) thinks that a mechanism for the absorption of chlorides from the surrounding medium exists in fresh-water fishes; but these authors have not provided satisfactory evidence for this view. From the fact that the chloride cells are abundantly present in some of the fresh-water teleosts, it is difficult to escape the conclusion that extra-renal excretion (i.e. excretion of chlorides by the gills) occurs in fresh-water teleosts.

Liu (1942) has suggested that 'the occurrence of the supposedly dormant chloride-secreting cells in the gills of fresh-water teleosts probably indicates
that the progenitors of the fresh-water fishes once inhabited the seas'. I have found chloride cells to be present in certain Indian species of fresh-water fishes in an active state and not in a dormant condition.

Smith (1931) and Bevelander (1935) have questioned the nature of the cells that perform this 'electrolyte excretion' in the gills of fishes and think that the whole of the respiratory epithelium of the gill lamellae might be involved in this work (of excretion). But histochemical tests have disclosed the presence of only a limited number of epithelial cells concerned in this 'electrolyte excretion'. Histological studies of fresh-water fishes by the present author have shown that mucous-gland cells excreting chlorides occur in the gill epithelium of some species of fresh-water fishes. The chloride tests, when applied to 8 Indian species of fresh-water fishes, belonging to different genera and families, succeeded in the case of 5 species only (see table 2), in which the mucous glands responded positively to the test. This result is contrary to that obtained by Keys and Willmer (1932), Liu (1942), and Copeland (1948a, b), who found the chloride-secreting cells to be essentially non-mucoid in character. The discovery of the presence of actively secreting chloride cells in certain species of fresh-water teleosts and their mucous nature are, therefore, new results.

According to the theory of osmo-regulation, extra-renal excretion of chlorides is to be expected only in marine fishes, and an interesting situation is created by the discovery of 'chloride cells' in certain fresh-water teleosts. The test for chloride is very positive in some fresh-water species of teleosts; in others it is less marked, but a silver network was found to exist in all the species examined. These obvious differences can be reconciled by assuming that the hypertonicity of the blood and of other body fluids of the different species of fresh-water fishes varies within a certain range, so that chloride cells are called into play according to the needs of the fish. It seems probable that the silver network is due to the presence of chlorides in the intercellular-cementing substance.

H. W. Smith (1931) was aware of chloride excretion in fresh-water fishes, and remarked that 'it is a very primitive process . . . being common to fresh- and salt-water teleosts'.

I wish to record my thanks to Prof. A. B. Misra for the interest he has taken in the progress of this work and for enlightening me from time to time with his knowledge of the problem. He has also taken pains to examine my microscopical preparations and to correct the manuscript of this paper. This work was done by me during the tenure of a Government of India Scholarship at the Banaras Hindu University.

References

—— 1936. Ibid., 59, 215.
Burns, J. and Copeland, D., 1950. Ibid., 99, 381.
Smith, H. W., 1930. Amer. J. Physiol., 93, 480.
— 1931. Ibid., 98, 279.
## Appendix

### Table I

**Summary of the tests**

<table>
<thead>
<tr>
<th>Species</th>
<th>Mucous glands</th>
<th>Multinucleated eosinophil and glandular cells</th>
<th>Response to chloride test</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Hilsa ilisha</td>
<td>+</td>
<td>-</td>
<td>only silver network present</td>
</tr>
<tr>
<td>2. Gadusia chapra</td>
<td>+</td>
<td>-</td>
<td>test not carried out</td>
</tr>
<tr>
<td>3. Catla catla</td>
<td>++</td>
<td>-</td>
<td>mucous glands responsive</td>
</tr>
<tr>
<td>4. Labeo rohita</td>
<td>++</td>
<td>-</td>
<td>test not carried out</td>
</tr>
<tr>
<td>5. Rohtee cotto</td>
<td>+</td>
<td>-</td>
<td>test not carried out</td>
</tr>
<tr>
<td>6. Clarias batrachus</td>
<td>+</td>
<td>+</td>
<td>some of the mucous glands are responsive</td>
</tr>
<tr>
<td>7. Heteropneustes fossilis</td>
<td>+</td>
<td>+</td>
<td>some of the mucous glands are responsive</td>
</tr>
<tr>
<td>8. Rita rita</td>
<td>+</td>
<td>++</td>
<td>only silver network present</td>
</tr>
<tr>
<td>9. Walago attu</td>
<td>+</td>
<td>+</td>
<td>test not carried out</td>
</tr>
<tr>
<td>10. Mystus aor</td>
<td>+</td>
<td>+</td>
<td>test not carried out</td>
</tr>
<tr>
<td>11. Ophiocephalus striatus</td>
<td>++</td>
<td>-</td>
<td>Some of the mucous glands responsive; silver network present</td>
</tr>
<tr>
<td>12. Ophiocephalus punctatus</td>
<td>++</td>
<td>-</td>
<td>some of the mucous glands are responsive</td>
</tr>
<tr>
<td>13. Trichogaster fasciatus</td>
<td>-</td>
<td>-</td>
<td>test not carried out</td>
</tr>
<tr>
<td>14. Anabas testudineus</td>
<td>+</td>
<td>-</td>
<td>test not carried out</td>
</tr>
<tr>
<td>15. Mastacembalus armatus</td>
<td>++</td>
<td>-</td>
<td>only silver network present</td>
</tr>
</tbody>
</table>

**General conclusions**

- Generally present in most of the species
- Present only in the siluroids
Table 2
Result of the chloride test

<table>
<thead>
<tr>
<th>Species</th>
<th>Mucous cells</th>
<th>Result of the chloride test applied to the mucous glands</th>
<th>Silver network reaction</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Hilsa ilisha</td>
<td>Present</td>
<td>No response</td>
<td>Present</td>
<td>Mucous glands do not respond to the chloride test</td>
</tr>
<tr>
<td>2. Catla catla</td>
<td>Abundantly present</td>
<td>Most of the mucous glands respond</td>
<td>Present</td>
<td>Mucous glands respond to chloride test</td>
</tr>
<tr>
<td>3. Clarias batrachus</td>
<td>Present</td>
<td>Some of the mucous cells respond</td>
<td>Present</td>
<td>Some of the mucous glands respond to the chloride test</td>
</tr>
<tr>
<td>4. Heteropneustes fossilis</td>
<td>Present</td>
<td>Some of the mucous cells respond</td>
<td>Present</td>
<td>Some of the mucous glands respond to the chloride test</td>
</tr>
<tr>
<td>5. Rita rita</td>
<td>Present</td>
<td>No response</td>
<td>Present</td>
<td>The mucous glands do not respond to the chloride test</td>
</tr>
<tr>
<td>6. Ophiocephalus striatus</td>
<td>Abundantly present</td>
<td>A few of them respond</td>
<td>Present</td>
<td>A few of the mucous glands respond to the chloride test</td>
</tr>
<tr>
<td>7. Ophiocephalus punctatus</td>
<td>Abundantly present</td>
<td>A few of them respond</td>
<td>Present</td>
<td>A few of the mucous glands respond to the chloride test</td>
</tr>
<tr>
<td>8. Mastacembalus armatus</td>
<td>Abundantly present</td>
<td>No response</td>
<td>Present</td>
<td>Mucous glands do not respond to the chloride test</td>
</tr>
</tbody>
</table>